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Biological species limits in the Cettia fortipes complex

by D. R. Wells

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On classical museum characters alone sections of the genus Cettia (sensu Delacour 1942-43) are among the trickiest of all sylviine warblers to identify. Their subdued brown plumages seem bereft of characters that could function as recognition marks in nature and visual cues may rank subordinate to signals of other kinds, such as vocalisations. Descriptions of Cettia songs in the literature (Ali & Ripley 1973, King et al. 1975, Neufeldt 1971, Smythies 1953) suggest a diversity well up to the sylviine average and a tendency also to unusual, arresting quality, confirmed in those described here. Through experiments with tape-recordings (this study; J. L. Gulledge, in litt.), songs have been shown to be important for territorial advertisement in the C. fortipes group, and among birds whose extreme skulking behaviour must reduce most visual contact to close-range encounters in dim light, they could also promote reproductive isolation. A taxonomic value is indicated (Lanyon 1969) and though I have found no reference to previous applications in Cettia, Dowsett & Stjernstedt (1979) have recently used song patterns to help resolve species limits in the related Bradypterus.

Delacour's reviews of these genera united under the name Cettia fortipes (Hodgson) the marginally tropical Sino-Himalayan bush warblers C. f. fortipes, pallidus and davidianus with 6 forms: oreophila, banksi, sepiaria, flaviventris (=sumatrana), vulcania (=montana) and everetti of the Sunda-Wallacea archipelago, linked via a small suite of morphometrical characters and seen as varying mainly in colour intensity with latitude. There are relatively few published natural history observations on any of these forms, especially from the southern range, but all those for which data are recorded do appear to select equivalent habitats, close to the ground in dense elfin forest, low thickets or rank herbage, always above 1000-2000 m altitude (e.g. Ali & Ripley 1973, Chasen & Hoogerwerf 1941). On Timur the endemic everetti is exceptional in having been collected from above 1500 m

down to 150 m (Mayr 1944, AMNH), at times of year when seasonal shifts of altitude range would not have been expected.

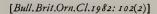
An insular niche-release of this type might have influenced dispersal locally, but most spread by the group has probably involved chance hopping between upland habitat-islands. With decreasing latitude, the continental Southeast Asian mountain summits nevertheless soon lose the appropriate indigenous vegetation zone (cf. Robbins & Smitinand 1966) and only in the Malay Peninsula does montane elfin forest reappear, at an altitude determined by the perhumid maritime climate. It closely resembles habitat now occupied in the Greater Sunda islands, but may not have been so continuously available because of the past situation of the Peninsula in the interior of a, now drowned, Pleistocene Sunda continent. Former Malayan populations, if they ever existed, could then have been eliminated through lack of refugia in the form of sufficiently high massifs and/or areas of mountain vegetation modified by vulcanism as in Indonesia. Assuming no other dispersal route, therefore, north-south gene-flow may have been hindered over a long period, and Delacour's inclusive arrangement accords poorly with the finding that, despite appearance and ecology, Sino-Himalayan and at least some Sunda-Wallacean forms possess sharply different songs.

New data here on vocalisations are drawn from my own field-notes and recordings and the tape collections of Dr. J. T. Marshall and the Cornell University Library of Natural Sounds. Representative cuts from tapes of pallidus in Kashmir and NW Frontier province, Pakistan, of fortipes in eastern Nepal, davidianus on Taiwan, oreophila on Mt Kinabalu, northwestern Borneo, and vulcania on Mt Pangrango, western Java, were sonographed. A comparative series of wide-band sonograms is given in Figure 1 and basic acoustic measurements are summarised in Table I.

The Sino-Himalayan forms, pallidus, fortipes and davidianus, all open with a held note of increasing energy but even pitch, at between about 1.5 and 3.2 KHz. This is followed immediately by an explosive pulse of brief, strongly modulated notes varying in number inversely with the length of the held note so that the full phrase is of fairly constant duration: 1640–2120 ms in Pakistan and 1480–1930 ms on Taiwan, at opposite longitudinal extremes of the range. Verbalisations cited by Ali & Ripley (1973) for pallidus and fortipes: 'he'll . . . beat-you', 'wheeeeee . . . chiwiyou', etc., fit my own impression of fortipes found in garden thickets at Darjeeling in late March 1971, when I noted down a song as peeee . . . piui.

Individual songs in Borneo and Java are shorter by up to one second and are a continuous whine, frequency-modulated throughout, with a subterminal crescendo that varies in shape but always spans a lesser range of frequencies than the explosive pulse of the northern song. Those of *oreophila* heard and taped on Mt Kinabalu in April 1975 typically opened with a brief grace-note, evident in the sonograms and loudest at about 4 KHz. This is represented by the first syllable of the verbalisation 'witch-a-wee-cheee-wee' given by Smythies (1981), which mistakenly fragments the succeeding whine but still gives a fair total impression of the *oreophila* song. In April 1978 entirely similar sounding vocalisations, as yet unsonographed, were taped in elfin forest on the upper slopes of Mt Mulu, type locality of banksi, in north Sarawak.

The limited tape and sonograph material of vulcania from west Java





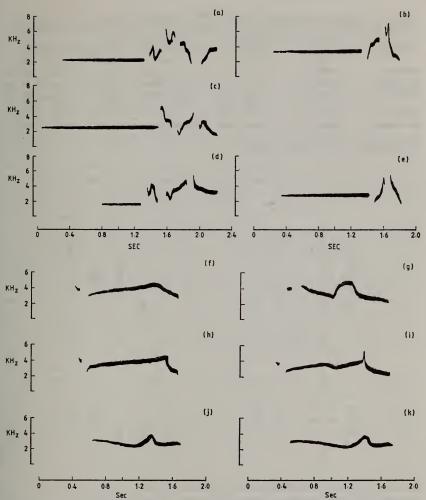


Fig. 1a. Broad band-width sonograms of sample songs in the Cettia fortipes complex: (a) and (b) pallidus (Kagan and Sind valleys, Pakistan), (c) fortipes (Arun valley, Nepal), (d) and (e) davidianus (Taiwan).

(f)-(i) oreophila (variants from the repertoire of one individual on Mount Kinabalu, Sabah), (j) and (k) vulcania (Mount Pangrango, Java).

includes no songs with an introductory grace-note but this song form does occur within the range of vulcania on Bali. Thus a bird seen at Kintamani, central highlands, on 17 April 1973 gave a song which I noted down at the time as chee-hu-ueeeoo, a five-part impression directly equatable with Smythies' description from Kinabalu. Such a difference could be dialectic at most – and just as these Sunda island songs show a high degree of relatedness, so the contrasting Sino-Himalayan song has survived isolation on Taiwan in at least equivalent detail (Fig. 1). In all instances geographical contact may have been lost by the end of the Pleistocene and the internal consistency of

TABLE 1
Some acoustic measurements of songs by bush warblers in the Cettia fortipes complex

	Number of	First note	Full phrase			
Taxon	notes1	duration	duration	Frequency (KHz)		
	(n)	(ms)	(ms)	Base	Peak	Śpan
vulcania	one (3)		1160–1280	2.5	3.8-3.9	1.3-1.4
oreophila	one (8)		1060-1270	2.3-3.0	4.5-5.2	1.5-2.6
pallidus	three (4)	1200-1400	1640-1820	1.8-2.1	5.2-6.4	3.4-4.4
•	five (4)	940-1200	1780-2120	1.8-2.1	5.4-6.0	3.6-4.1
fortipes	four (2)	1580-1640	2280	1.5-1.8	5.3-5.8	3.8-4.1
davidianus	three (4)	1060-1540	1480-1930	1.5-1.9	4.0-5.5	2.6-3.7
	four (1)	660	1540	2.I	4.7	2.6

¹Excluding introductory grace-notes.

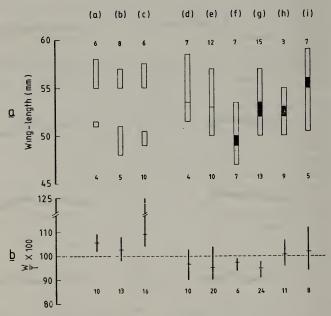


Fig. 2. Morphometric differences in the Cettia fortipes complex.

a. Male (upper column) and female (lower column) wing-length ranges, and

b. Wing-length/tail-length indices (range and mean):
(a) pallidus, (b) fortipes, (c) davidianus, (d) palawana, (e) oreophila, (f) everetti, (g) vulcania, (h) flaviventris and (i) sepiaria. Sample sizes are given opposite relevant ranges.

the 2 song patterns, each traversing a minimum 3 named morphological forms, implies an important genetic break.

Two small and unrelated morphometrical differences match this break. Male and female wing-length ranges were found to be separated by gaps of 3.5-4.5 mm in samples of the Sino-Himalayan forms, but were contiguous to broadly overlapping in 6 Sunda-Wallacean forms measured (Fig. 2a), including the recently discovered Philippine palawana. A wing-length:taillength ratio (W/T x 100) likewise sorted 91 out of 99 specimens in the combined measurable sample (other than from Sumatra) to above or below value 100,

respectively, for Sino-Himalayan and Sunda-Wallacean groupings (Fig. 2b). Samples of 11 flaviventris, including the type (Violani 1980) from southern Sumatra, and 8 sepiaria from Mt Leuser in Aceh province were intermediate on this second character.

For these various reasons it is suggested that Cettia fortipes as constituted by Delacour is a probable composite, most sensibly restricted to include, of the named forms, only pallidus, fortipes and davidianus. These replace each other west to east in the Himalayan, north Burmese (Thailand) and south China uplands, from Pakistan to Taiwan. Records on conjoined hill-tracts in northern Vietnam, northern Laos and the Sittang-Salween divide at Nattaung peak (18° 49'N) (BMNH, King et al. 1975) probably also refer to this species, and could include an additional subspecies (Smith et al. 1944), though this has never been formally described. The specimen in question, from Nattaung, was collected in long grass fringing a hill road and no habitat now occupied that far south in continental Asia is likely to pre-date clearance of the mountain forest by man. Status there is uncertain.

It follows from this action that an additional species must be recognised to accommodate, in the first instance, oreophila and banksi of Borneo and vulcania of Java and Bali as agreeing on a combination of characters including distinctive vocalisations, or on these vocalisations alone. The position of the Lombok island population of vulcania, east of Bali, is problematical in that only 2 specimens were measured and its song is unknown; indeed, there are no records subsequent to the original collection of a century ago. Sumatran forms, palawana of Mt Mantalingajan, Palawan island, and everetti from Timur likewise conform on one or both of the morphometric characters, but until their songs are described can be only provisionally allocated to this

second species.

The name adopted for it must be Cettia vulcania (Blyth) 1870 Java if under Article 11 of the International Code it is accepted that, as first describer, Blyth acquired authorship of a manuscript name he himself attributed to Solomon Müller (Delacour 1947). As pointed out by others (e.g. Phillips 1968) the more widely used name for the Javan bird, montana Horsfield 1821, is a primary homonym of Sylvia montana Wilson 1812, applied to a parulid warbler.

'Strong-footed Bush Warbler' remains valid as a vernacular name for the Sino-Himalayan species since it was coined for nominate *fortipes* prior to Delacour's revision. 'Müller's Bush Warbler' is proposed as a new and suitably commemorative name for *C. vulcania*. Other recent English names apply across species and should be abandoned for this reason.

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A confirmation of the specific relations of Cuculus saturatus insulindae Hartert

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Becking (1975) and Wells & Becking (1975) invoked details of plumage, beak morphology, egg-shell appearance and ultrastructure, vocalisations and brood parasitism to show that C. lepidus, a small Cuculus resident in montane forests from Sumatra and peninsular Malaysia to the Lesser Sunda islands, is a diminutive Oriental Cuckoo C. saturatus and not, as widely assumed, a subspecies of C. poliocephalus. The eggs and brood hosts of a similar Bornean cuckoo, insulindae, are unknown but the few specimens examined in the above study shared critical morphology and plumage characters with both lepidus and northern subspecies of C. saturatus. C. insulindae was tentatively transferred to saturatus after taking into account the additio nalevidence of vocalizations commonly heard on Mount Kinabalu, Sabah, in February-March (Smythies 1959) and an evidently similar sound described on the label of a specimen from Kinabalu in the collection of the Sarawak Museum, Kuching.

During a visit to Kinabalu National Park 28-30 March 1975 I was able to satisfy myself that these vocalisations were one and the same. A lepidus-like call was heard repeatedly in lower montane forest at around 1500 m altitude. It was tape-recorded and the calling bird attracted to a play-back proved, as guessed, to be a small Cuculus fitting the description of insulindae. In April 1978 identical calls were heard at around 1300 m on Mount Mulu, Sarawak,

about 180 miles SW of Kinabalu.